REVISION OF THE NEOTROPICAL GENUS ISCHYOMIUS WITH A DISCUSSION ON ITS SYSTEMATIC POSITION (INSECTA: COLEOPTERA: TENEBRIONOIDEA: PYTHIDAE)

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ABSTRACT

The Neotropical genus *Ischyomius* Chevrolat is reviewed and comprises six species: *I. singularis* Chevrolat, *I. denticollis* Champion, *I. chevrolati* Champion, *I. bicolor* Champion, *I. nevermanni*, new species (Costa Rica, Limón Province), and *I. championi*, new species (Ecuador, Pichincha Province). The following new synonymies are proposed: *Pseudoischyomius* Pic 1923 = *Ischyomius* Chevrolat 1878; *Pseudoischyomius rufipennis* Pic 1923 = *Ischyomius bicolor* Champion 1916. Primary types were examined for all species, and lectotypes are designated for *I. singularis* and *I. chevrolati*. The systematic placement of *Ischyomius* is discussed, and based on structure of male and female genitalia, the genus is placed in the family Pythidae, provisionally near *Sphalma* Horn.

KEY WORDS: insects, Coleoptera, Tenebrionoidea, Pythidae (Ischyomius), Neotropics

INTRODUCTION

The Neotropical genus Ischyomius Chevrolat, like other enigmatic taxa within Tenebrionoidea, never has had a stable family placement. The genus was described by Chevrolat (1878) in Tenebrionidae, near Acropteron Perty. Champion (1886) retained this position, and created the "Ischyomiides," stating that many features of Ischvomius differed significantly from Acropteron and other tenebrionids. Later, Champion (1889) transferred Ischyomius to Melandryidae, based on possession of open procoxal cavities. This new placement was reflected in Champion's (1916) treatment of Melandryidae, in which Ischyomius is placed in the Ischyomiina, after the genus Synchroa Newman. Beginning with Csiki (1924), Ischyomius was placed in the Tetratominae (Melandryidae), near Synchroa. This was followed by Blackwelder (1945), Crowson (1955) as Tetratomidae, and Arnett (1983). Lawrence (1982) placed the genus in Pythidae without explanation, but stated that it was a very distinct group. Watt (1987) moved Ischyomius into Trictenotomidae based on adult similarities exhibited between the two taxa. Pollock (1994) stated, in the absence of detailed analyses, that Ischyomius belonged in Pythidae, based on structural similarities in male and female genitalia. This hypothesis was adopted by Pollock and Lawrence (1995). Lawrence and Newton (1995) treated the genus as Pythidae, incertae sedis.

This paper presents a taxonomic revision of *Ischyomius*, in which evidence is presented for the placement of the genus in Pythidae, provisionally near *Sphalma* Horn.

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MATERIALS AND METHODS

Collection abbreviations used in the text are: AAAC, Albert A. Allen collection, Boise, Idaho; BMNH, The Natural History Museum, London, United Kingdom; CASC, California Academy of Sciences, San Francisco, California; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CNC, Canadian National Collection of Insects, Ottawa, Ontario, Canada; DAPC, Darren A. Pollock private collection, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; FSCA, Florida State Collection of Arthropods, Gainesville, Florida; INBC, Instituto Nacional de Biodiversidad (INBio), Heredia, Costa Rica; MNHN, Entomologie, Muséum National d'Histoire Naturelle, Paris, France; MUCR, Museo de Insectos, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D. C.; OXUM, Hope Entomological Collections, Oxford University Museum, Oxford, United Kingdom; RHTC, Robert H. Turnbow, Jr. Collection, Fort Rucker, Alabama; SEMC, Snow Museum, University of Kansas, Lawrence, Kansas; SMTD, Staatliches Museum für Tierkunde, Dresden, Germany.

The techniques used for specimen preparation and study are the same as those explained in Pollock (1995). Type specimens were examined for all species of *Ischyomius*; label data are enclosed in quotes and individual labels are separated by a slash (/). Measurements are presented in millimeters, as follows: HL—length of head between anterior margin of labrum and anterior margin of pronotum; GHW—maximum width around head, across eyes; PL—length of pronotum along midline; GPW—maximum width across pronotum; EL—length of elytron from humerus to apex of spine; GEW—maximum width across both elytra; TL—sum of HL and PL and EL.

TAXONOMIC ACCOUNTS

Genus Ischyomius Chevrolat, 1878

Ischyomius Chevrolat, 1878:98; Champion, 1886:258; Champion, 1893:548; Champion, 1916:81;
Seidlitz, 1916:387; Seidlitz, 1917:88 (as Ischiomius); Csiki, 1924:6; Blackwelder, 1945:494;
Crowson, 1955:113, 132; Lawrence, 1982:544; Arnett, 1983:2; Watt, 1987:115; Pollock, 1994:
522; Pollock and Lawrence, 1995:466, 468; Lawrence and Newton, 1995:897. Type species,
Ischyomius singularis Chevrolat, by monotypy.

Pseudoischyomius Pic, 1923:21; Blackwelder, 1945:494. Type species, Pseudoischyomius rufipennis Pic, by monotypy. New synonymy.

Diagnosis.—Specimens of Ischyomius may be distinguished from other genera of Pythidae based on the following character states (also see key in Pollock and Lawrence [1995]): mandibles with lateral flange (Fig. 2A, D); pronotum wide, at least indistinctly explanate laterally, with distinct lateral carina; tarsomeres 1–4 (1–3 on hind legs) lobed (Fig. 3D), densely setose ventrally; elytra widest anteriorly, distinctly tapered posteriorly (Fig. 1).

Description.—Body (Fig. 1) elongate (TL/GEW 3.5-4.3), flattened slightly dorsoventrally, widest anteriorly and narrowed posteriorly; TL 5.9-13.4; GEW 1.5-3.8.

Head relatively short and wide, narrowed behind eyes; eyes large, relatively coarsely faceted, emarginate slightly near antennal insertions; frontoclypeal suture indicated laterally, medially marked by transversely sunken area; labrum transverse, anterior margin slightly emarginate to truncate; antennae elongate, antennomeres subserrate to filiform, slightly to moderately flattened. Mandibles (Fig. 2, 3B) large, prominent, slightly asymmetrical; apices unidentate, with small ventral accessory tooth situated posterior of apex; ventral lateral flange distinct, extended from accessory tooth to basal point of articulation; terebral teeth (Fig. 2E:t) short, blunt; both mandibles with dorsal carina (Fig. 2D:dc),

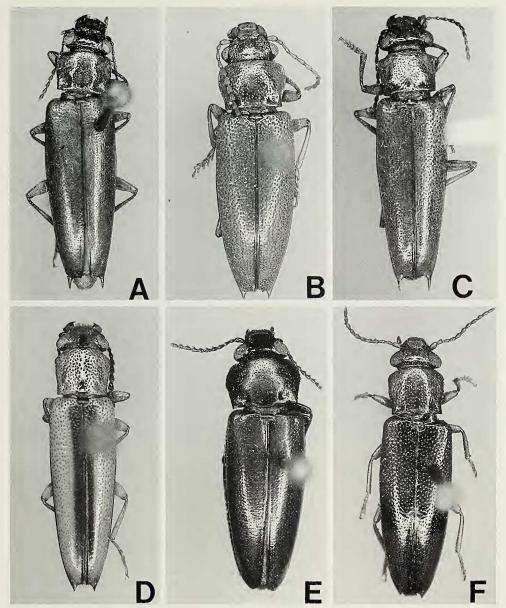


Fig. 1.—Dorsal habitus of *Ischyomius* species. A, *I. singularis* Chevrolat (TL 11.7 mm); B, *I. chevrolati* Champion (TL 9.9 mm); C, *I. denticollis* Champion (TL 10.1 mm); D, *I. championi*, n. sp. (TL 9.5 mm); E, *I. bicolor* Champion (TL 10.6 mm); F, *I. nevermanni*, n. sp. (TL 8.7 mm).

significantly more distinct on right mandible; ventral microtrichia (Fig. 2B:mi) elongate, extended posteriorly onto distinct prostheca (Fig. 2F:p); mola (Fig. 2C:m; 3B) distinct, subtriangular, concave and convex on left and right mandible, respectively; occlusal surface of mola composed of rows of minute asperities. Maxilla with large, subtriangular galea, fringed with dense, fine setae; lacinia reduced in size, fringed apically with long setae; apical maxillary palpomere securiform (Fig. 3A). Mentum (Fig. 3A) distinctly transverse, anterior margin evenly arcuate or slightly lobed; distinct pit

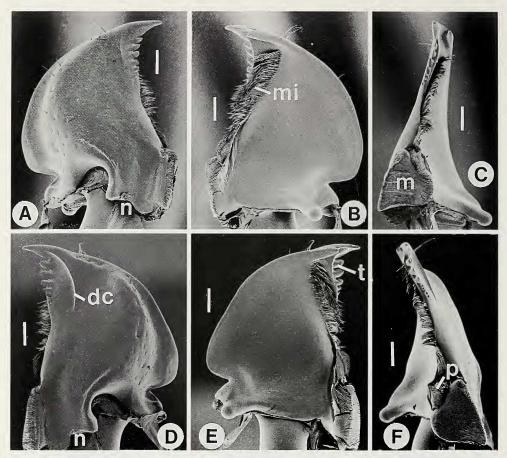


Fig. 2.—Mandibles of adult *Ischyomius chevrolati*. A, left mandible, dorsal; B, left mandible, ventral; C, left mandible, occlusal; D, right mandible, dorsal; E, right mandible, ventral; F, right mandible, occlusal. dc = dorsal carina, m = mola, mi = microtrichia, n = basal notch, p = prostheca, t = terebral tooth. Scale bar = 0.1 mm.

(Fig. 3A:p) in mentum in males of two species. Labium with apical palpomere similar in shape to maxillary palp, slightly securiform (Fig. 3A).

Prothorax wider than long, widest anteriorly; pronotal disc slightly and more or less evenly convex, with small depressions posterolaterally; disc slightly explanate laterally in one species (*I. singularis*); lateral edge of pronotal disc smooth (Fig. 4C) or with small tubercles (Fig. 4A); lateral pronotal carina distinct along entire lateral margin; posterior pronotal margin with or without distinct bead, at least vaguely bisinuate; prosternum anterior of coxae distinct; prosternal process (Fig. 3C) distinctly produced posteriorly between coxae; apex of process broadly rounded and margined; procoxae rounded, not extending significantly below process; procoxal cavities open externally and internally; protrochantins concealed.

Elytra elongate (Fig. 1), about 2.3–2.8 times longer than wide; sides subparallel anteriorly, then narrowed posteriorly; lateral margins visible dorsally or narrowly concealed; humeri distinct; disc evenly convex; epipleuron distinct, wide anteriorly, narrowed posteriorly, traceable to, or just anterior of, apical spine; apex of elytra with variously acute spine, indistinct in one species; scutellum transverse, broadly rounded posteriorly; mesosternum narrowly separating mesepisterna, sloping from anterior margin to intercoxal process; mesocoxae separated narrowly, trochantin concealed or barely visible between lateral extensions of meso- and metasternum; mesocoxal cavities closed partly by mesepimeron; metasternum convex, without distinct median line; metendosternite (Fig. 6) with mod-

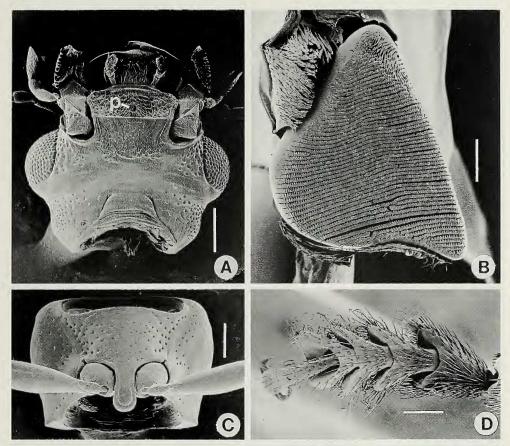


Fig. 3.—Structural features of adult *Ischyomius* spp. A, *I. singularis*, head, ventral view; B, *I. chevrolati*, detail of right mandibular mola; C, *I. chevrolati*, prothorax, ventral view; D, *I. singularis*, foretarsus, dorsal view. p = mental pit. Scale bar = 0.5 mm (A), 0.05 mm (B), 0.4 mm (C), 0.2 mm (D).

erately long, broad stalk; anterior tendons inserted on elongate arms distal of midlength; laminae broad, rounded laterally.

Hind wing (Fig. 5) with relatively short membrane; veins indistinctly pigmented (shown dark in figure for clarity); area beyond radial cell about 0.3 times as long as entire wing; radial cell distinct, small; medial region with four terminal veins; wedge cell narrow, elongate.

Legs slender, femora expanded slightly toward midlength; tibiae very slightly widened apically; apex of tibiae with row of stout setae; tibial spurs short, stout; inner apical surface of tibia with moderately dense brush of setae, especially distinct on fore tibiae; all but last tarsomere expanded laterally, triangular; tarsomeres (Fig. 3D) distally slightly emarginate, ventral surface with dense setae; apical tarsomere narrow, relatively elongate; tarsal claws relatively long and slender.

Abdomen with all segments freely articulated; ventral surfaces more or less uniformly punctate, with or without setae; tergite 8 broadly rounded apically; tergite 8 shallowly, broadly rounded apically; sternite 8 shallowly emarginate; sternite 9 in males with elongate spiculum gastrale.

Aedeagus (Fig. 7, 8B) with tegmen oriented dorsad of median lobe; basale subequal in length to apicale, or with apicale distinctly longer than basale; apicale variously narrowed to near apex, cleft slightly; accessory lobes short and angular, to slender and elongate, rounded or slightly spatulate distally, with setae basally and apically; parameral struts present, membranous towards, and articulated with, base of median lobe; median lobe parallel-sided, slender, apex evenly tapered, distinctly sclerotized along lateral margins only; tegmenite distinct, subquadrate, adpressed tightly against basale.

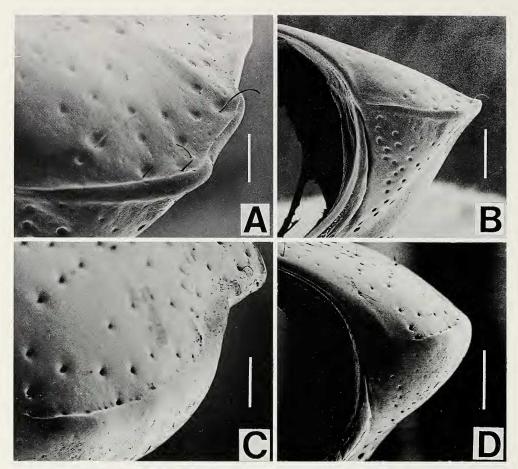


Fig. 4.—Prothoraces of *Ischyomius* spp. A, *I. singularis*, pronotal disc, anterolateral oblique view; B, *I. singularis*, prothorax, anterior view; C, *I. chevrolati*, pronotal disc, anterolateral oblique view; D, *I. chevrolati*, prothorax, anterior view. Scale bar = 0.1 mm (A, C), 0.2 mm (B, D).

Ovipositor (Fig. 8A) elongate, flexible; coxites three-segmented, apical segment distinctly longer than basal two; coxites sparsely setose, more so distally; two pairs of elongate baculi distinct; spiculum ventrale elongate, subequal or slightly greater in length than ovipositor; styli spindle-shaped. Internal reproductive tract (Fig. 8A) with two-chambered bursa copulatrix (Fig. 8A:b), distal chamber cleft slightly, possibly forming spermatheca (Fig. 8A:s); slender, elongate spermathecal gland (Fig. 8A:g) attached by narrow duct to distal chamber (= spermatheca).

Natural History.—Little has been published on the biology or habits of species of Ischyomius. Champion (1916) stated that specimens of I. chevrolati were common in dead banana leaves in Panama. The information below was derived from the label data of specimens examined. Specimens of I. chevrolati were collected from wilted foliage of several species of Musaceae: Musa sapientum L. (banana), M. paradisiaca L. (plantain), and M. textilis Née. This species was found among banana debris at several quarantine interception points in the USA. Most of the individuals of I. singularis were collected by beating dry banana leaves on a plantation. Specimens of I. nevermanni, new species, were taken from foliage of two genera of Palmae: Cryosophila (= Acanthorrhiza) warscewiczii (H. Wendl.)

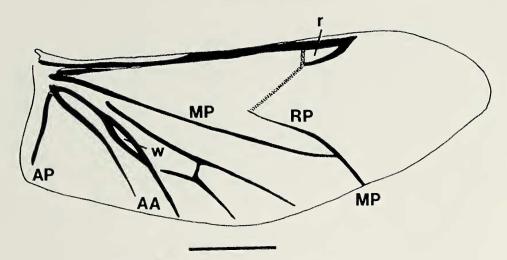


Fig. 5.—Flight wing of *I. singularis*. Scale bar = 2 mm.

Bartlett and Iriartea sp. A specimen of Ischyomius bicolor was collected in a fallen palm (Orbigna phalerata Martius) frond in Brazil.

Distribution.—The species of *Ischyomius* exhibit a Neotropical distribution, with a range that extends from Costa Rica, through Panama, into northwestern South America as far south as central Brazil (the latter based on one potentially dubious record).

KEY TO SPECIES OF ISCHYOMIUS CHEVROLAT

		Pronotum with distinct bead along entire posterior margin (in most specimens); abdominal ventrites 1–4 with obvious vestiture
2		Antennomeres filiform; elytral apex with conspicuous, outer spine (Fig. 1A-D, F) 3 Antennomeres short, subserrate; elytral apex without conspicuous, outer spine (Fig. 1E)
3	(2).	Antennomeres 2–10 piceous to black, contrasting in color to antennomeres 1 and 11; lateral margins of pronotum with several long setae; body testaceous, with median, longitudinal dark vitta extended from frons to elytral apex (Fig. 1D)
	3'.	Antennomeres 1–11 concolorous, rufous; lateral margins of pronotum without long setae; body testaceous to rufous with elytral infuscation, around scutellum and rectangular to diamond-shaped, transverse dark area slightly posterior of elytral midlength (Fig. 1F)
4		Anterolateral angles of pronotum produced, square to slightly acute (Fig. 1C)
5	(4').	Lateral margins of pronotal disc evenly arcuate (Fig. 4C); lateral pronotal bead not at-
	5′.	taining anterior pronotal margin (Fig. 4D); lateral margins evenly convex to edge
		pronotal margin (Fig. 4B); lateral margins explanate, flat to slightly concave to lateral edge

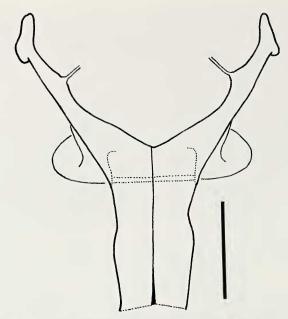


Fig. 6.—Metendosternite of *I. singularis*. Scale bar = 0.5 mm.

Ischyomius singularis Chevrolat (Fig. 1A; 3A, D; 4A, B; 5; 6; 7D; 10)

Ischyomius singularis Chevrolat, 1878:98; Champion, 1916:81; Csiki, 1924:6; Blackwelder, 1945:494.

Type Specimens.—Lectotype, here designated, female, labelled: "[green label with illegible handwritten locality] / Muséum Paris 1906 Coll. L. FAIRMAIRE / [red label] TYPE / [handwritten] Ischyomius singularis Chev Bogota", (MNHN, coll. Fairmaire). Paralectotype male, labelled: "[green label] N Grenad Honda Goudon / Muséum Paris 1906 Coll. L. FAIRMAIRE / [red label] TYPE" (MNHN, coll. Fairmaire).

Taxonomic Notes.—One specimen from OXUM bears the label "Amphora complanata de Brême." This specimen was mentioned by Champion (1916) as having been given to the BMNH in 1871 as part of the Bowring Collection. Although the label on this specimen predates Chevrolat's description, Champion states that Amphora complanata is a manuscript name only and he does not question the validity of *I. singularis. Amphora* is already twice pre-occupied in zoology, once for an echinoderm and once for a weevil (Neave, 1939). Another specimen in BMNH has the label "Amphora sec. Doué's coll." I have been unable to find a citation for *A. complanata*, and it is here discarded as an available name.

Diagnosis.—Ischyomius singularis is one of the three unicolorous species in the genus. Its diagnostic features include the mental pit in the male (Fig. 3A) and carinate lateral pronotal margin (Fig. 4A, B). Ischyomius singularis is structurally similar to I. denticollis, but lacks the produced anterolateral pronotal angles of the latter. Pronotal features separating I. singularis and I. chevrolati are given in the key.

Description.—TL 6.9-13.4; GEW 1.8-3.5. Color uniformly rufotestaceous to rufopiceous. Eyes relatively small, nonprotuberant; antennae relatively long, antennomeres 5-10 filiform, elongate; male

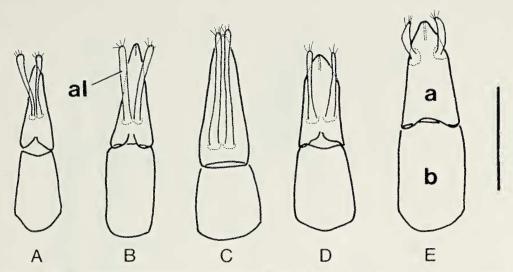


Fig. 7.—Aedeagi of *Ischyomius* spp., median lobe removed, dorsal. A, *I. bicolor*; B, *I. nevermanni*, n. sp.; C, *I. chevrolati*; D, *I. singularis*; E, *I. denticollis*. a = apicale, al = accessory lobe, b = basale. Scale bar = 0.5 mm (A-D), 0.8 mm (E).

with pit on mentum; dorsal punctation relatively coarse, sparse, shallow. Pronotum wider than long (GPW/PL 1.2–1.4), without elongate, erect setae; posterior bead absent; lateral margin of disc variously crenulate, or tuberculate, widest anterior of midlength; anterolateral angles rounded; disc relatively flat, slightly explanate to lateral margins, with distinct posterolateral depressions; lateral carina distinct, present to anterior margin; punctation relatively shallow, irregular. Elytra without regular, erect setae; apical spine very long; punctation fine, shallow. Tarsomeres (all but distal) greatly expanded. Venter of abdomen without distinct vestiture. Aedeagus relatively stout, with apicale subequal in length to basale; apicale broad, almost parallel-sided; accessory lobes relatively elongate, inserted proximad to apicale midlength.

Other Material Examined.—BOLIVIA. Country record only, (SMTD, 1). COLOMBIA. Magdalena: San Sebastian de Rabago, Sierra Nevada de Santa Marta, 2000 m, 11–14.iv.1968, B. Malkin, beating dry banana leaves on plantation, (FMNH, 43); same locality, except 12–13.iv.1968, ex dry banana leaves on banana plantation, (FMNH, 28). Valle: nr. Pichinde, 5000′, 18.vii.1970, H. & A. Howden, (CNC, 1). Country records only, (OXUM, 1), (BMNH, 2). ECUADOR. Bolivar: Balzapamba, 1500 m, (MNHN, 3). Chimborazo: Chimbo [= Puente de Chimbo], M. de Mathan, 1891, (MNHN, 2). Napo: Lago Agrio (41 Kms. W.), 18.v.1975, Spangler et al., Ecuador–Peace Corps–Smithsonian Institution Aquatic Insect Survey, (NMNH, 1); Limoncocha, 250 m, 9–16.iii.1976, J. M. Campbell, (CNC, 2). Pastaza: Cusuimi, Rio Cusuimi, 150 km SE Puyo, 300 m, 15–31.v.1971, B. Malkin, (FMNH, 2); same data, except 300 m, 18–23.vii.1971, (FMNH, 1); 8 km NE Puyo, 28.iv.1978, C. W. & L. B. O'Brien & Marshall, (FSCA, 1). Pichincha: 47 km SE Sto. Domingo, Rio Palenque Sta., 300 m, 22–28.ii.1976, J. M. Campbell, (CNC, 1). PERU. Huánuco: Yurac, 67 mi E. of Tingo Maria, 11.xii.1954, E. I. Schlinger & E. S. Ross, (CASC, 1). Lima: Callanga, (FMNH, 8), (NMNH, 2). General locality (not mapped). Nova Grenada, (BMNH, 1).

Geographical Distribution.—All examined specimens of I. singularis were collected in northwestern South America (Fig. 10).

Ischyomius chevrolati Champion (Fig. 1B; 2; 3B, C; 4C, D; 7C; 8; 11)

Ischyomius chevrolati Champion, 1916:82; Csiki, 1924:6; Blackwelder, 1945:494.

Type Specimens.—Lectotype, male, here designated, left specimen on card with two specimens, labelled: "V. de Chiriqui, 25-4000 ft. Champion. / [round label

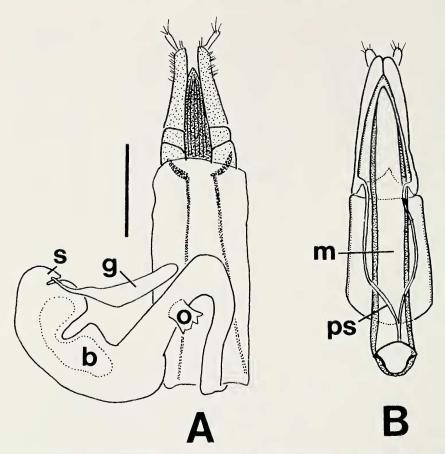


Fig. 8.—A, ovipositor and reproductive tract of female l. chevrolati; B, aedeagus of l. chevrolati, ventral. b = bursa copulatrix, g = spermathecal gland, m = median lobe, o = oviduct, ps = parameral strut, s = spermatheca. Scale bar = 0.5 mm.

with red margin] Type H. T. / [male and female biological symbols] / Ischyomius chevrolati, Ch / B.C.A. Col. IV. 2. Ischyomius singularis Chev. Champ. / [round label with blue margin] SYNTYPE" (BMNH). Paralectotype, female, mounted on same card as lectotype. Two paralectotypes, mounted on one card, one female, the other sex indeterminate, labelled: "V. de Chiriqui, 25–4000 ft. Champion. / B.C.A. Col. IV. 1. Ischyomius singularis Chev. Champ. / Ischyomius singularis Chevr. / [round label with blue margin] SYNTYPE" (BMNH).

Ischyomius singularis Champion (not Chevrolat) 1886:259, pl. 11, fig. 17 and 17 a, b, c.

Diagnosis.—Ischyomius chevrolati is recognized by the following features: body unicolorous; males without mental pit; pronotum with lateral margin smooth, carina dorsal (Fig. 4C, D). Among the other unicolorous species of *Ischyomius, I. chevrolati* lacks the produced anterolateral pronotal angles of *I. denticollis* (Fig. 1C) and has a different pronotal structure than *I. singularis* (Fig. 4A, B).

Description.—TL 7.7-11.4; GEW 2.2-3.2. Color uniformly rufotestaceous. Eyes relatively small, nonprotuberant; antennae long, antennomeres filiform, relatively elongate; male without pit on mentum; punctation relatively coarse, more or less uniformly spaced. Pronotum wider than long (GPW/

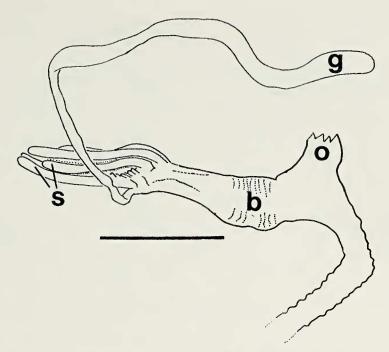


Fig. 9.—Reproductive tract of female Trictenotoma sp. b = bursa copulatrix, g = spermathecal gland, o = oviduct, s = spermatheca(e). Scale bar = 1 mm.

PL 1.3–1.4), without elongate, erect setae; posterior pronotal bead absent; lateral margin of disc smooth, parallel-sided basally, and evenly arcuate to anterior margin; anterolateral angle rounded; disc relatively convex, not explanate laterally, with slightly developed posterolateral depressions; lateral carina indistinct, not present to anterior margin; punctation relatively shallow. Elytra without regular, erect setae; apical spine moderately long; punctation deep and coarse. Tarsomeres (all but distal) moderately expanded. Venter of abdomen without distinct vestiture. Aedeagus relatively slender, with basale distinctly shorter than apicale; apicale evenly tapered apically; accessory lobes very long and slender, inserted toward base of apicale.

Other Material Examined.—COSTA RICA. Cartago-Limón border: 40 km NE Turrialba, 500 m, 18.v.1979, H. & A. Howden, (CNC, 1). Limón: Valle de la Estrella, Valle de Rosas, nr. Pandora, 17.ii.1984, H. & A. Howden, (DAPC, 1); Finca Hamburgo, F. Nevermann, (MUCR, 1); Hamburg Farm, Reventazon Ebene, Limon, 26.x.1934, F. Nevermann, welkem Blatt von Musa sapientum, (NMNH, 1); same data, except 28.xii.1934, (NMNH, 3); same data, except 20.ix.1935; same data, except 3.xi.1927, (NMNH, 3); same locality, 25.x.1934, welkem Blatt von Musa paradisiaca, (NMNH, 1); same locality, 6.ii.1928, an welkem Bananenblatt, (NMNH, 1); same locality, 30.vii.1934, an welkem Laub Musa textilis, (NMNH, 1); same locality, 20.ix.1935, welkem Blatt von Musa sapientum, (NMNH); Las Mercedes, Sta. Clara, 200-300 m, 6.viii.1922, F. Nevermann, (NMNH, 1); Guapiles, Sta. Clara, 250-300 m, 22.iv.1935, welkem Blatt von Musa sapientum, F. Nevermann, (NMNH, 1); Las Mercedes, 12.vii.1922, F. Nevermann, (NMNH, 1). Puntarenas: Osa Peninsula, habitat near Sirena, 0-5 m, xi.1983, S. H. Boinski, (CMNH, 1); same locality and collector, v.1984, coll. on living foliage in second growth forest, (CMNH, 2); same locality and collector, xi.1983, coll. on dead foliage, (CMNH, 2; DAPC, 1); viii.1984, second. forest with bamboo, coll. on dead foliage, (CMNH, 2; DAPC, 1); viii.1984, coll. on dead foliage in second growth forest, (CMNH, 1); vi.1984, ex. sweep sample in second growth forest, (CMNH, 1); vi.1984, coll. on dead foliage in secondary growth forest, (CMNH, 1; DAPC, 1); Monteverde, 1400 m, 23.v.1979, H. & A. Howden, (CNC, 4); same locality, 21. viii. 1987, H. & A. Howden, (DAPC, 1). San José: Coronado, 1400-1500 m, 15. viii. 1931, F. Nevermann, welkem Blatt von Musa sapientum, (NMNH, 1); San José, 1000-1100 m, 26.viii.1928, F. Nevermann, (NMNH, 2); San Jose, 19.vi.1962, L. Berkeley, woodland farmland window, night, (FSCA, 1). Quarantine records: on banana debris, ex Costa Rica, N.Y. 46434, (NMNH, 2); on banana

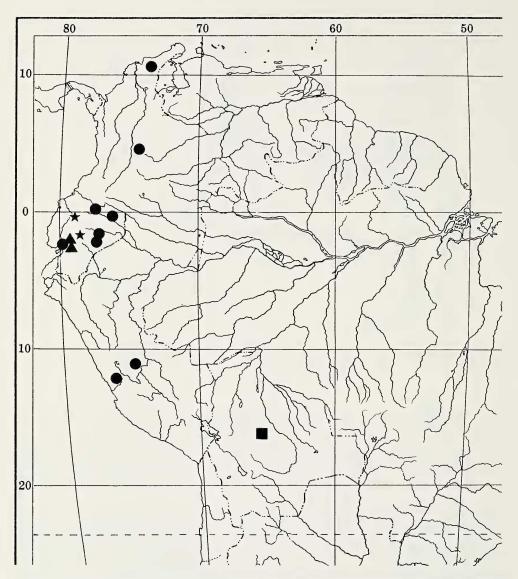


Fig. 10.—Known distribution of *I. singularis* (dots and stars) and *I. denticollis* (triangles and stars). Square represents country record (Bolivia) for *I. singularis*.

trash, ex Costa Rica, N.Y. No. 23993, (NMNH, 1); on banana ex Costa Rica 8.vii.1935, N.Y. 44942, (NMNH, 1). Locality not found or mapped: San Vito, 25.v.1983, (AAAC, 1). PANAMA. Canal Zone: Frijoles, on Musaceae, E. A. Schwarz, (NMNH, 1). Chiriquí: 2 km N. Sta. Clara, 1300 m, Hartmann's Finca 8°51'N 82°46'W, 20.v.1977, H. & A. Howden, (CNC, 4); Hartmann's Finca, 19.v.1996, R.Turnbow, (RHTC, 2); V. de Chiriqui, 25–4000 ft., Champion, (NMNH, 4); 27.7 km W. Volcan Hartmann's Finca 08°45'N, 82°48'W, 1450 m, 14–17.vi.1995, J. Ashe & R. Brooks, ex slash, (SEMC, 1); Fortuna Dam, 16.v.1992, E. Giesbert, (FSCA, 1). Quarantine records: on banana debris ex Panama, 14.i.1937, Mobile 5581, (NMNH, 1); ex Panama Mobile Al 29.i.1934, in debris of banana Mob. # 1852, S. S. Sheffield, (NMNH, 1); Panama, 24.iv.1931, B. Bryant, on banana S. F. # 2585, (NMNH, 3). VENEZUELA. State unknown: Los Camales [= Canales?], G. Vivas B., (FMNH, 1).

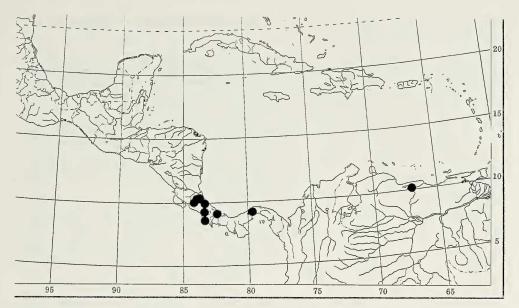


Fig. 11.—Known distribution of I. chevrolati.

Geographical Distribution.—All but a single examined specimen of *I. chevrolati* were collected in Costa Rica and Panama (Fig. 11). A single record is known from northern Venezuela, based on a questionable locality. "Los Camales" has here been interpreted as a misspelling of "Canales," and mapped accordingly.

Ischyomius bicolor Champion (Fig. 1E; 7A; 12)

Ischyomius bicolor Champion, 1916:82; Csiki, 1924:6; Blackwelder, 1945:494.

Type Specimen.—Holotype, sex unknown, labelled: "Sarayacu, Ecuador. C. Buckley. / [label with horizontal green line through middle] Sarayacu 80.14 / [round label with red margin] Type H. T. / Ischyomius bicolor, Ch' (BMNH).

Pseudoischyomius rufipennis Pic, 1923:21; Blackwelder, 1945:494.

Type Specimen.—Holotype, sex unknown, labelled: "Iguapo / [yellow label] type / [red label] TYPE / Museum Paris coll. M. Pic / Pseudoischyomius n gen rufipennis n sp", (MNHN). New synonymy.

Taxonomic Notes.—Two forms of I. bicolor were examined in this study. All but one of the specimens agreed very closely with the types of both I. bicolor and Pseudoischyomius rufipennis. One specimen, however, is considerably shorter and exhibits characters not found in the other specimens. Notably, the lateral margins of the pronotal disc have several crenulations in the anterior half and the body color is atypical (see diagnosis below). I judged this individual to be an aberrant specimen of I. bicolor, although discovery of additional material may necessitate a closer examination of its status.

Diagnosis.—Ischyomius bicolor is the only species in the genus with relatively short, serrated antennae, and lacking the apical elytral spine. Also, in all but one specimen, the pronotal color is dark and contrasts that of the elytra. In the one

aberrant specimen the pronotum and elytra are concolorous, the latter with an infuscate area along the suture.

Description.—TL 7.9–12.1; GEW 2.3–3.4. Color of two forms; typical: head and pronotum piceous, elytra rufous; atypical: body rufous with area along elytral suture infuscated, not extended to apex. Eyes large, protuberant; antennae relatively short, antennomeres 5–10 moniliform/subserrated; males without pit on mentum; punctation fine, relatively sparse. Pronotum distinctly wider than long (GPW/PL 1.4–1.5), with few long marginal setae; posterior pronotal bead distinct; lateral margins of disc subparallel-sided basally, arcuate anteriorly; lateral margin with several crenulations in anterior half in one specimen (see taxonomic notes); anterolateral angle rounded; disc slightly convex, not explanate; lateral carina distinct, present to anterior margin; punctation relatively shallow. Elytra with several rows of erect setae, especially toward lateral margin; apical spine very short, indistinct. Tarsomeres moderately expanded. Venter of abdomen with distinct vestiture. Aedeagus slender, with apicale very slightly longer than basale; apicale slender, evenly tapered apically; accessory lobes slender, enlarged apically, inserted slightly proximal of midlength of apicale.

Other Material Examined.—BRAZIL. Amazonas: São Paulo de Olivença, M. de Mathan, (MNHN, 1). Rondônia: 62 km. SW Ariquemes, Fzda. Rancho Grande, 11.xi.1994, C. W. & L. B. O'Brien, in fallen frond babaçu palm, Orbigna phalerata Martius, (DAPC, 1). COLOMBIA. Amazonas: Leticia, 700', 10.vii.1970, H. & A. Howden, (CNC, 4). ECUADOR. Pastaza: Cusuimi, Rio Cusuimi, 150 km SE of Puyo, 15–31.v.1971, B. Malkin, (FMNH, 1). PERU. Loreto: Iquitos, M. de Mathan, (MNHN, 2). Madre de Dios: Tambopata Wildlife Res, 30 km SW Pto. Maldonado, 12°50'S, 69°20'W; 290 m,

9.xi.1982, J. J. Anderson, (CMNH, 1).

Geographical Distribution.—Ischyomius bicolor is found in NW South America, and its aggregate range extends further east and south than the other South American species of the genus (Fig. 12). The type specimen of *Pseudoischyomius rufipennis* was collected in "Iguapo." A search of atlases and gazetteers failed to locate such a locality. However, there are four separate populated places in Brazil called "Iguape" (two in Bahia and one each in Espirito Santo and São Paulo), one of which might represent the type locality of *P. rufipennis*.

Ischyomius denticollis Champion (Fig. 1C; 10)

Ischyomius denticollis Champion, 1916:81; Csiki, 1924:6; Blackwelder, 1945:494.

Type Specimen.—Holotype, male, labelled: "44 / [green label] 160 / [round label with red margin] Type H. T. / [label upside down] 71.6 / [handwritten, partly illegible label, something like "pres du uloma"] / Ischyomius denticollis, Ch" (BMNH).

Diagnosis.—Ischyomius denticollis is recognized easily by the produced anterolateral pronotal angles (Fig. 1C). Males of *I. denticollis* possess the large mental pit found also in *I. singularis*. The structure of the aedeagus (Fig. 7E) of *I. denticollis* is unique in *Ischyomius*: the accessory lobes are very short, curved, and inserted toward the distal end of the apicale.

Description.—TL 10.6–12.3; GEW 2.7–3.2. Color uniformly rufotestaceous. Eyes large, protuberant; antennae moderately long, antennomeres 5–10 filiform, relatively elongate; male with pit on mentum; punctation fine, sparse, shallow. Pronotum distinctly wider than long (GPW/PL 1.3–1.4), without elongate, erect setae; posterior pronotal bead absent; lateral margin of disc smooth, widest at anterolateral angle; anterolateral angle produced, acute; disc convex, not explanate laterally, with slightly developed posterolateral depressions; lateral carina distinct, present to anterior margin; punctation relatively shallow, more or less regularly spaced. Elytra without regular, erect setae; apical spine very long; punctation moderately coarse. Tarsomeres (all but distal) moderately expanded. Venter of abdomen without distinct vestiture. Aedeagus stout, apicale and basale subequal in length; lateral margins of apicale slightly convergent apically; accessory lobes short, curved, inserted near distal end of apicale.

Other Material Examined.—ECUADOR. Bolivar: Balzapamba, iii-iv.1894, M. de Mathan,

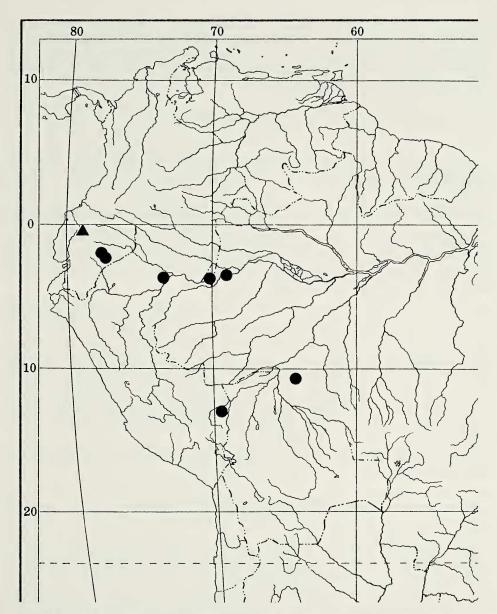


Fig. 12.—Known distribution of I. bicolor (dots) and I. championi, n. sp. (triangle).

(MNHN, 5); Balzapamba, Route de Quito, vii-viii.1893, M. de Mathan, (MNHN, 1). Esmeraldas: Cachabé [= Cachavi], xi.1896, Rosenberg, (MNHN, 1); same data except xii.1896, (MNHN, 1); Cachabé to Paramba [Imbadura Prov.], ii.1897, Rosenberg, (MNHN, 2). Los Ríos: Pichilingue, 40 m, 2.ii.1955, E. I. Schlinger & E. S. Ross, (CASC, 1). Pichincha: Rio Palenque, 47 km S. St. Domingo, 700′, 22.ii.1976, H. & A. Howden, (CNC, 1). Country unknown: Manizales, A. M. Patino, (MNHN, 1).

Geographical Distribution.—All examined specimens of *I. denticollis* with reliable label data were collected in Ecuador (Fig. 10). Champion (1916) tentatively gives the locality of the type of *I. denticollis* as Colombia, although there is no

indication of this on the specimen. This specimen was obtained by BMNH in 1871 along with specimens of *I. singularis*, which were collected in Colombia (Champion 1916). This record is not included on Figure 10. A specimen from MNHN was collected at Manizales; since there is a Manizales in both Colombia and Ecuador, this record is not mapped.

Ischyomius championi, new species (Fig. 1D; 12)

Type Specimen.—Holotype, sex unknown, labelled: "Ecuador, Pich. 47 Km SE Sto Domingo Rio Palenque Sta. II.22–28.1976 300 m J. M. Campbell" (CNC).

Derivation of Specific Epithet.—This species is named in honor of George C. Champion (1851–1927), who was a pioneer in the systematics of *Ischyomius* and many other groups of Tenebrionoidea.

Diagnosis.—Among Ischyomius, this species is unique in having the body color testaceous with a central dark vitta extending from the head to near elytral apex (Fig. 1D). The only other constantly maculate species, I. nevermanni, has the contrasting color pattern on the elytra only.

Description.—TL 9.5; GEW 2.2. Color testaceous with antennomeres 2–10 piceous; antennomere 11 rufous; dorsum with narrow, longitudinal black vitta starting between eyes and extended to elytral apex, along suture. Eyes large, protuberant; antennae long, antennomeres 5–10 short, submoniliform; male with or without pit on mentum (single specimen examined of undetermined sex); punctation coarse, irregularly spaced. Pronotum relatively elongate (GPW/PL 1.1), with several elongate, marginal setae; posterior pronotal bead distinct; lateral margins of disc subparallel-sided with few fine crenulations on each side; anterolateral angle rounded; disc moderately convex, not explanate laterally, with indistinct posterolateral depressions; lateral carina distinct, curved dorsally before attaining anterior margin; punctation deep, coarse, relatively uniformly spaced. Elytra with rows of regular, erect setae, especially on lateral areas; apical spine relatively short. Tarsomeres moderately expanded. Venter of abdomen with distinct vestiture. Aedeagus not studied.

Geographical Distribution.—The holotype of I. championi was collected in western Ecuador (Fig. 12).

Ischyomius nevermanni, new species (Fig. 1F; 7B; 13)

Type Specimens.—Holotype, male, labelled: "[green label] COSTA RICA F NEVERMANN 15.XI.26 / [green label, inverted] HAMBURGFARM REVENTAZON EBENE LIMON / [illegible handwritten label]" (NMNH). [Specimen dissected with abdomen mounted on card and genitalia in microvial beneath specimen]. Allotype, female, labelled: "[green label] COSTA RICA F NEVERMANN 25 X 35 / [green label, inverted] HAMBURGFARM REVENTAZON EBENE LIMON / an welkem Laub [with handwritten name]" (NMNH). Thirty-eight paratypes, sexes not determined. Twenty-six from same locality as holotype (DAPC, 1; CMNH, 1; FMNH, 2; NMNH, 22). Other paratypes as follows: COSTA RICA. Cartago: Turrialba, 650 m, 25.ii.1980, H & A Howden, (CNC, 1). Guanacaste: 2 mi. N. Bijagua, 13.ix.1990, 430 m, B. C. Ratcliffe, (DAPC, 1). Heredia: La-Selva, nr. Pto. Viejo 50 m 19.Feb.1980, H & A Howden, (CNC, 2). Limón: Guápiles, 6.x.1915, F. Nevermann, (NMNH, 4); Bananito, 20.iv.1925, F. Nevermann, (MUCR, 1); Escosia, 12.vi.1928, F. Nevermann, (MUCR, 2); Est. Cuatro Esquinas, 0 m, P. N. Tortuguero, xii.1992, R. Delgado, (INBC, 2). PANAMA.

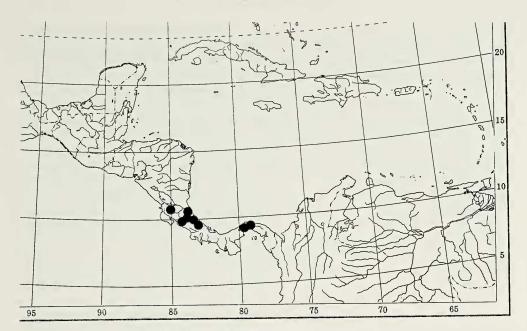


Fig. 13.—Known distribution of I. nevermanni, n. sp.

PortoBello [= Portobelo], 28.ii.1911, E A Schwarz, (NMNH, 1). *Panama*: Parque Nacional Soberania, 23.v.1996, R. Turnbow, (RHTC, 2).

Derivation of Specific Epithet.—This species is named in honor of cucujid specialist Wilhelm Heinrich Ferdinand Nevermann, who collected most of the type material.

Diagnosis.—Ischyomius nevermanni is recognized easily by its maculate color pattern, expanded laterally on the elytra only (Fig. 1D). The only other species of *Ischyomius* with a distinct elytral macula is *I. championi*, in which the macula is linear and unexpanded laterally, and extends from the head to the elytral apex.

Description.—TL 5.9–10.5; GEW 1.5–2.8. Color testaceous to rufous; elytra with triangular, median infuscation along suture, expanded into transverse fascia, reaching or closely approaching lateral margins. Eyes very large, distinctly protuberant; antennae long, antennomeres 5–10 filiform, relatively short; male without pit on mentum; punctation relatively fine, sparse. Pronotum moderately elongate (GPW/PL 1.1–1.2), without distinct, marginal setae; posterior pronotal bead distinct, slightly indistinct medially in a few specimens; lateral margins of disc relatively straight, evenly divergent anteriorly, with or without shallow sinuations; anterolateral angle rounded; disc moderately convex, not explanate laterally, with indistinct posterolateral depressions; lateral carina distinct, not present to anterior margin; punctation moderately coarse, evenly spaced. Elytra with few scattered erect setae; apical spine relatively short. Tarsomeres only slightly expanded. Venter of abdomen with distinct vestiture. Aedeagus relatively slender, apicale slightly longer than basale; apicale evenly tapered to apex; accessory lobes slender, inserted basally on apicale.

Geographical Distribution.—Ischyomius nevermanni is known only from Costa Rica and Panama (Fig. 13). The record from Guanacaste Province represents the most northern record for the genus.

Systematic Placement of *Ischyomius*Familial Affinities

Analytical Approach.—Evidence is presented here to support the placement of Ischyomius within Pythidae, rather than Trictenotomidae, as suggested by Watt

(1987). The presence of parameral struts (Fig. 8B:ps) on the male genitalia places *Ischyomius* within the unresolved (Pythidae + Salpingidae + Trictenotomidae) clade of the salpingid group of families (Pollock, 1994). The following adult structural features define further the placement of *Ischyomius*.

Pit on Male Mentum.—Males of all Pythinae, except Anaplopus Blackburn, possess a small, circular to elliptical deep pit(s) of unknown function, through which often protrude a number of stiff setae or microtrichia (e.g., Pollock, 1991: fig. 5C, D; Young, 1976:fig. 9–11). Males of at least I. denticollis and I. singularis (Fig. 3A:p) have a similar pit. This feature is unknown in other examined members of the salpingid group, and, although not present in all species of Ischyomius, it still may be a synapomorphy for Pytho Latreille, Priognathus LeConte, Sphalma Horn, and Ischyomius. The pit is presumed lost in Anaplopus Blackburn and the remaining four species of Ischyomius (condition unknown in I. championi, n. sp.).

Structure of Internal Female Reproductive Tract.—Pollock (1994) stated that the presence of a double-chambered bursa copulatrix is a synapomorphy uniting genera of Pythidae. Pollock and Lawrence (1995) stated that all species they examined representing the genera of Pythidae possess the double-chambered bursa copulatrix. This was in error, because the bursa copulatrix in females of Sphalma is actually single-chambered. This may represent a reversal of the apomorphic state present in all other genera of Pythidae. The bursa copulatrix in Ischyomius is double-chambered (Fig. 8A:b), while in Trictenotoma Blanchard it is elongate and single chambered (Fig. 9:b).

Arrangement of spermathecae and accessory glands was shown to be important in classifying constituents of the salpingid group (Watt, 1987; Pollock, 1994, 1995). Two different types of spermathecae are found in Pythidae. In one type, including *Ischyomius* and *Sphalma*, the spermatheca is formed by a narrowing of the distal chamber of the bursa copulatrix (Fig. 8A:sp). The spermatheca in *Pytho* and *Priognathus* is undifferentiated. In *Trictenotoma*, the spermatheca is divided into six relatively short, elongate branches, in three groups of two (Fig. 9:sp).

In most species of Pythidae, an accessory gland is present, joined to one of the two chambers of the bursa copulatrix (e.g., Pollock and Lawrence, 1995:fig. 17). This gland is absent from representatives of two species groups of *Pytho*, however. Females of *Ischyomius* have an elongate accessory gland (Fig. 8A:g). Females of *Trictenotoma* have a very long elongate accessory gland (Fig. 9:g) attached to the distal end of the bursa copulatrix.

Additional research is needed to resolve fully the homologies among the various structures of the internal female reproductive tract within the Tenebrionoidea, and specifically, the salpingid group. However, the presence of the double-chambered bursa copulatrix and the structure of the accessory gland suggest an affinity of *Ischyomius* with Pythidae.

Structure of Male Genitalia.—An analysis of male genitalia similarly indicates an affinity of Ischyomius with Pythidae, rather than Trictenotomidae. Taxa of both families exhibit basic structural similarities of the male genitalia and were thought to be closely related by Pollock (1994). The two main parts of the tegmen, the basale and apicale (Fig. 7E:b and a), are of more or less equal length in pythids. In trictenotomids the basale is very short, and the apicale is about four times the length of the basale (Sharp and Muir, 1912). In Ischyomius, the paired accessory lobes (Fig. 7B:al) articulated to the apicale are relatively short, and are with few, short apical setae. In males of Trictenotomidae, the accessory lobes are very long, with long, dense, apical setae (Sharp and Muir, 1912). Within the salpingid group,

the presence of parameral struts (as opposed to basal struts) on the aedeagus was thought to be a synapomorphy of (Trictenotomidae + Salpingidae + Pythidae) by Pollock (1994). Males of *Ischyomius* have distinct parameral struts (Fig. 8B: ps) that are membranous towards the base of the median lobe, and a basally cylindrical aedeagus characteristic of other Pythidae.

Structural Differences Between Ischyomius and Other Pythidae.—In addition to the above similarities between Ischyomius and other Pythidae, there are certain important differences, including the size and shape of the procoxal process and the shape of the tarsomeres. All other taxa of Pythidae have a relatively short procoxal process, not extended posterad of the coxae (e.g., see Pollock, 1991:fig. 7A, B). The procoxal process in Ischyomius is larger, expanded posteriorly, and extends behind the procoxae (Fig. 3C). Adults of Pytho, Priognathus, Sphalma, and Anaplopus have simple, unexpanded tarsomeres, while those of Ischyomius are distinctly widened (Fig. 3D).

Conclusion.—Although admittedly aberrant, *Ischyomius* should be retained in Pythidae and not in Trictenotomidae as suggested by Watt (1987). Discovery and description of the larva of *Ischyomius* will be extremely important in either corroborating or refuting this family placement.

Position of Ischyomius Within Pythidae

Pollock and Lawrence (1995) discussed the constituents of Pythidae and some of the more important characters defining the genera. However, they did not provide a detailed phylogenetic analysis of the characters. In spite of this, some speculative comments regarding the placement of *Ischyomius* within Pythidae are presented here.

Among other genera of Pythidae, *Ischyomius* shares several features with *Sphalma*. In both genera, the antennal insertions are concealed dorsally (Pollock and Lawrence, 1995); this feature is most distinct in *Sphalma*. In species of both genera, the mandibular mola is very large (Fig. 2C:m; 3B; Pollock, 1995:fig. 25), with the prostheca (Fig. 2F:p) proximal and distal to it (this type of mola is found also in *Anaplopus* [Pollock and Lawrence, 1995:fig. 10]). Also, dorsally on the mandibular base, there is a notch just lateral of the mola (Fig. 2A, D:n), that among pythids is found only in *Ischyomius* and *Sphalma*. The lateral pronotal carinae in *Ischyomius* and *Sphalma* are distinct, and visible dorsally for their entire lengths. The pronotum in *Pytho*, *Priognathus*, and *Anaplopus* is smooth, without lateral carinae.

From this and other studies on genera of Pythidae, the following three groups (these are not yet proven to be monophyletic) are postulated: 1) Sphalma and Ischyomius, 2) Pytho and Priognathus, and 3) Anaplopus. According to Pollock and Lawrence (1995), the genera Osphyoplesius Winkler and Trimitomerus Horn should be placed also in Pythidae; discovery and/or description of the larvae of these two genera will strengthen or refute their placement. The phylogenetic relationships among these genera will form the subject of subsequent research in this family.

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